# Antibiosis and Antixenosis to *Aphis gossypii* (Homoptera: Aphididae) in *Colocasia esculenta*

JENIFER L. COLESON[1] AND ROSS H. MILLER

Agricultural Experiment Station, College of Natural and Applied Sciences, University of Guam, Mangilao, Guam 96923

J. Econ. Entomol. 98(3): 996–1006 (2005)

**ABSTRACT** Fifty cultivars of taro, *Colocasia esculenta* (L.) Schott (Araceae), collected from islands in Micronesia and Polynesia, eight cultivars from the University of Hawaii's taro germplasm collection, and a closely related aroid, *Xanthosoma sagittifolium* (L.) (Araceae), were screened for antibiosis and antixenosis to *Aphis gossypii* Glover. Life history data for *A. gossypii* were collected by assessing survivorship and fecundity of aphids caged on taro leaves in the field. Significant differences in aphid reproductive rate and longevity were observed among the taro cultivars, and cultivars were ranked from most resistant to most susceptible. Antixenosis was assayed in the laboratory in a multiround choice test where *A. gossypii* were offered four leaf discs excised from different taro cultivars. Additionally, field observations of aphid abundance on taro cultivars were made to corroborate clip cage studies and laboratory experiments. 'Iliuaua', 'Rumung Mary', 'Maria', 'Ketan 36', and 'Agaga' were the most resistant in terms of reducing aphid fecundity and survivorship, whereas the Iliuana, 'Purple', 'TC-83001', and 'Putih 24' were least preferred in aphid choice tests. *X. sagittifolium* consistently exhibited strong aphid resistance. Resistant cultivars identified in this study may form the basis of breeding programs seeking to combine aphid resistance with other desirable agronomic traits in taro.

**KEY WORDS** *Aphis gossypii*, *Colocasia esculenta*, *Xanthosoma sagittifolium*, host resistance, taro

TARO, *Colocasia esculenta* (L.) (Araceae), is a culturally important and profitable aroid commonly grown as a staple food crop throughout the tropical Pacific islands of Guam, Pohnpei, Tonga, Samoa, Kosrae, Yap, and Palau (Ferentinos 1993). In Hawaii, taro leaves are used as a green vegetable, whereas the corms are made into taro chips and poi, a sour tasting paste deeply rooted in Hawaiian culture and tradition (Onwueme 1999).

Taro is beset by a number of insect pests and diseases (Mitchell and Maddison 1983) that restrict its production in the Pacific and impede its expansion in the United States. Among the insects attacking taro, high populations of the melon aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), and the leafhopper *Tarophagus proserpina* (Kirkaldy) (Homoptera: Delphacidae) lower yield by feeding on plant fluids. Aphids and leafhoppers further foul the plant by secreting honeydew on leaves and stems which serves as a substrate for sooty mold and attracts ants. Aphid-tending ants protect aphid colonies on taro plants from predation by natural enemies that would otherwise maintain aphid populations at a low level (Starý 1970). They also disrupt farm activities by stinging farm personnel working in the taro fields.

*Aphis gossypii* is known to vector >50 plant viruses (Sylvester 1989), including a taro virus, Dasheen mosaic virus, found in the Pacific basin (Zettler et al. 1978). Taro leaf blight, *Phytophthora colocasiae* Raciborski (Pythiaceae), is an *A. gossypii*-vectored disease that originated in Java (Indonesia) and has subsequently spread throughout much of the Pacific region, including Micronesia and Polynesia. In Hawaii, *P. colocasiae* has reduced the number of commonly grown taro cultivars from 300 to ≈30 and has recently proved especially devastating to taro production in American Samoa and Samoa (SPC 1996).

Studies at the University of Guam suggest that significant differences exist in the severity of aphid infestations and in aphid life history parameters among *A. gossypii* populations infesting taro varieties grown on Guam (Miller and Wall 1999).

The purpose of this research was to identify sources of *A. gossypii* resistance in taro by using conventional field and laboratory screening methodologies. Resistant taro lines identified in this project will hasten the development of commercially suitable taro varieties for U.S. and Pacific region growers and will provide an array of germplasm types to be used in developing DNA probes for molecular marker-assisted selection.

## Materials and Methods

**Field Station Studies.** Experiments were conducted on the island of Guam, the largest and southernmost island of the Mariana Archipelago in the tropical western Pacific. Fifty cultivars of taro, collected from islands

[1] Natural Resources Conservation Service, United States Department of Agriculture, Barrigada Plaza Bldg., Suite 101, 494 West Route 8, Barrigada, Guam 96913.

**Table 1. Collection sites of taro cultivars**

| Cultivar | Collection site | Cultivar | Collection site |
|---|---|---|---|
| Apu 23 | Indonesia | Laatan Green | Rumung[c], Yap[b] |
| Ketan 36 | Indonesia | Laatan Red | Rumung[c], Yap[b] |
| Putih 24 | Indonesia | Mang Green | Rumung[c], Yap[b] |
| | | Mang Red | Rumung[c], Yap[b] |
| P-10 | Palau[a] | Maria | Rumung[c], Yap[b] |
| P-20 | Palau[a] | Purple | Rumung[c], Yap[b] |
| | | Rumung 1 | Rumung[c], Yap[b] |
| Dar 2 | Yap[b] | Rumung John | Rumung[c], Yap[b] |
| Dar 3 | Yap[b] | Rumung Lisa | Rumung[c], Yap[b] |
| Dar 4 | Yap[b] | Rumung Mary | Rumung[c], Yap[b] |
| Dar 8 | Yap[b] | Tamdad | Rumung[c], Yap[b] |
| Dar 10 | Yap[b] | Tamdad Yellow | Rumung[c], Yap[b] |
| Dar 11 | Yap[b] | | |
| Dar 12 | Yap[b] | Agaga | Guam |
| Fel (Feleng) | Yap[b] | Fiji | Guam |
| Gilin | Yap[b] | Japon | Guam |
| Gurumed | Yap[b] | Visaya | Guam |
| Gutep | Yap[b] | *X. sagittifolium* | Guam |
| Hana | Yap[b] | | |
| Kugfel | Yap[b] | Ahlahl Pohntipw | Pohnpei[d] |
| Laev | Yap[b] | Kosrae | Pohnpei[d] |
| Likay | Yap[b] | Pwetepwet | Pohnpei[d] |
| Mat | Yap[b] | SPC | Pohnpei[d] |
| Moyolyol | Yap[b] | Toantoal | Pohnpei[d] |
| Oglang | Yap[b] | Mang | Pohnpei[d] |
| Olyap | Yap[b] | | |
| Red Palauan | Yap[b] | Niue | American Samoa |
| Sushi | Yap[b] | | |
| Tinian | Yap[b] | Bun Long | Hawaii |
| Saipan | Yap[b] | Iliuaua | Hawaii |
| | | Okinawa | Hawaii |
| AG-1 | Rumung[c], Yap[b] | TC 83001 | Hawaii |
| John | Rumung[c], Yap[b] | White BL | Hawaii |

Taro collected from the islands of Yap and Rumung were donated by individual farmers to Dr. George Wall, University of Guam, whereas taro cultivars from Indonesia and Hawaii were provided by Dr. John Cho, Maui Agricultural Research Center, University of Hawaii.

[a] Republic of Palau.

[b] Yap State, Federated States of Micronesia.

[c] Rumung, Yap State, Federated States of Micronesia.

[d] Pohnpei State, Federated States of Micronesia.

in Micronesia and Polynesia, and eight cultivars from the University of Hawaii's taro germplasm collection (Table 1) were grown and maintained in the field and in pots under shade cloth. *Xanthosoma sagittifolium* (L.) Schott (Araceae), an aroid closely related to taro, was included in the study for comparison purposes because of its known aphid resistance (Rubatzky and Yamaguchi 1997, Miller and Wall 1999). Cultivars also were kept in tissue culture in the University of Guam's plant pathology laboratory. Field experiments were conducted at the University of Guam's Yigo Agricultural Experiment Station (13.31862° N, 144.52112° E) and Inarajan Experiment Station (13.28164° N, 144.75706° E). Soil samples were taken from the taro fields in Yigo and Inarajan and analyzed by the University of Guam Soil Laboratory. Soils in Yigo were clayey, gibbsitic, nonacid, isohyperthermic Lithic Ustorthents, whereas Inarajan soils were clayey, montmorillonitic, isohyperthermic, shallow Udic Haplustalfs (Young 1988).

Weather data were obtained from the National Weather Service Forecast Office, Tiyan, Guam (http://www.prh.noaa.gov/pr.guam.html) located near the Guam International Airport in central Guam, approximately equidistant from the Yigo and Inarajan experimental stations. Normals for Guam (1945–2002) and data for 2002 were compiled.

Taro was propagated vegetatively in pots and transplanted to the field in 20-m-long rows along a north-south axis during August and November 2001. All cultivars were grown using drip irrigation methods commonly used on Guam in upland taro cultivation. Taro plants were between 0.25 and 0.5 m in height when transplanted. Four individuals of each cultivar were planted together in a row at a 0.5-m spacing. At planting, 100 g of fertilizer (N–P–K; 16:16:16) was incorporated into the soil just below the root zone of each plant. At 2-, 4-, and 6-month intervals, a side dressing of 50 g of pelletized chicken manure (N–P–K; 5:3:1.5) was applied to each plant. No pesticides were used during the experiment. Taro was irrigated via automated drip line for 1 h each morning and 1 h each afternoon throughout the experiment. Weeding and desuckering were performed once per month on all plants.

Parthenogenically reproducing aphids used in the different trials of this study were reared on a single host cultivar to minimize the possibility of genetic variation between aphids within a trial. All aphids used in field experiments were reared on 'Ogland' for at least three generations before selecting first instars for inclusion in clip cage tests. After Typhoon Chata'an on 5 July 2002, the abundance of aphids in experiment station fields was very low for several months. The large quantity of aphids needed for the laboratory choice tests after this date made it necessary to collect aphids from a single unknown taro cultivar heavily infested with *A. gossypii* on one of the few nearby local farms that escaped damage from the typhoon.

**Assessment of Agronomic Traits.** Selected agronomic traits, including plant height, leaf span, leaf blade color, leaf vein color, petiole color, leaf waxiness, and overall plant vigor were evaluated for each taro cultivar and for *X. sagittifolium.* Assessments of taro planted in August and November 2001 were conducted during January and March 2002, respectively. Plant height, or the maximum vertical distance attained by leaves relative to the ground, was coded as follows: dwarf (<50 cm), medium (50–100 cm), and tall (>100 cm). Leaf span, or the maximum horizontal distance attained by leaves was coded as narrow (<20 cm), medium wide (20–30 cm), and wide (>30 cm).

Leaf blade color was determined by observing the second youngest fully expanded leaf. Leaf main vein color was observed on the lower side of the leaf blade beyond the junction of the petiole. Petiole color was observed roughly in the middle portion of the petiole. Leaf blade color, leaf vein color, and petiole color were coded as white, yellow green, green, dark green, pink, red, brown, and purple.

Leaf waxiness was categorized as low, medium, or high and determined by rubbing the second youngest fully expanded leaf between the thumb and forefinger.

Leaves with low waxiness were generally pliable and tender, whereas leaves with high waxiness were thick and durable. Plant vigor was based on observations of all four plants of each cultivar and ranked as poor, intermediate, or excellent. Plants with poor vigor were growing weakly, had poor leaf development, showed signs of chlorosis, and had little or no corm development. Plants with excellent vigor were growing robustly and had excellent corm development, and plants with intermediate vigor exhibited characteristics of both poor and excellent classifications.

**Abundance Ratings.** The population density of naturally occurring *A. gossypii* on field-grown cultivars was used to create aphid abundance ratings for different cultivars at the Yigo Experiment Station. Abundance ratings were performed once per month between January and May 2002. Aphid ratings were based on the most heavily infested plant of the four for each cultivar and were as follows: 0, zero aphids per leaf; 1, <75 aphids per leaf; 2, 76–200 aphids per leaf; and 3, >200 aphids per leaf. Ratings were averaged over the different sampling intervals, and taro cultivars were ranked from lowest to highest.

**Antibiosis Experiments.** Life table studies by using clip cages were conducted to determine antibiosis characteristics of taro cultivars. Because these studies were labor-intensive, the experiment was subdivided into separate trials. In total, 11 trials were conducted in 2002 at the Yigo Experiment Station from 11 January to 16 February, 29 January to 5 March, 8 February to 21 March, 17 February to 25 March, 1 March to 5 April, 8 March to 13 April, 22 March to 25 April, 29 March to 3 May, 23 April to 27 May, 11 May to 14 June, and 26 May to 26 June. One trial was conducted at the Inarajan Experiment Station from 28 May to 26 June 2002 on eight taro cultivars not available in the Yigo Experiment Station plots.

Clip cages were adapted from Adams and van Emden (1972). Fine gauze mesh was glued to one end of a 1.5-cm-wide by 1-cm-long section of Tygon tubing. The meshed side of the tubing was then glued to the inner surface of one arm of a 4.5-cm-long metal hair clip. A 3-cm-wide concave circular plastic disc was glued to the other tine so that a tight seal was made between the Tygon tubing and leaf surface when the cage was clipped onto a taro leaf.

In screening for antibiosis on taro, mature apterous *A. gossypii* females were placed in clip cages on the leaves of Ogland, a taro cultivar identified by Miller and Wall (1999) as being highly susceptible to *A. gossypii.* Newly born nymphs were collected after 24 h with a fine sable brush and placed in a small plastic cup until placed under a clip cage on the underside of a fully opened and mature taro leaf. Taro leaves showing signs of senescence were not used. A single aphid nymph was placed in each clip cage.

Each caged aphid was observed daily at approximately the same time each day. The number of offspring produced by each aphid during each observation period was recorded, as was any mortality and its suspected cause. Offspring born to aphids within the clip cages were removed when discovered, whereas

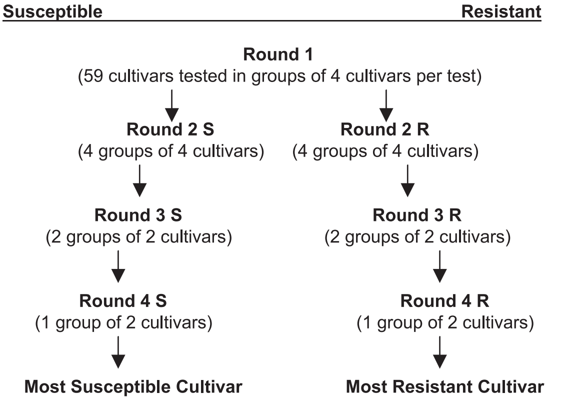


**Fig. 1.** Diagram of multiple-round trials to test for antixenosis resistance. In round 1 of the trial, cultivars in which the lowest number of total aphids had settled were advanced to round 2R (resistant), whereas cultivars in which the highest total number of aphids had settled were advanced to round 2S (susceptible). In rounds 2R and 3R, cultivars with the lowest number of aphids were advanced to the next round, whereas in rounds 2S and 3S cultivars with the highest number of aphids were advanced. The trial concluded in round 4, where a winner (most resistant cultivar) and a loser (most susceptible cultivar) were identified.

the mother aphid was retained. Each clip cage was checked daily until the enclosed aphid died or the clip cage was otherwise disturbed. Data collected from a given clip cage were not included in the analysis if that aphid was subject to a nonhost-related demise or escaped. Factors that caused a sample to be discarded from the analysis frequently included wind, predation by ants, or escape.

Mean longevity and mean fecundity for caged aphids were calculated on each of the 59 cultivars studied and used to rank cultivars from most resistant (lowest longevity and lowest fecundity) to least resistant (highest longevity and highest fecundity). Means, standard errors of the mean, coefficients of variation, and least significant differences (LSDs) [$LSD_{(df,\ \alpha)}$] were computed (Sokal and Rohlf 1995). Mean longevity and mean number of offspring produced by aphids caged on each cultivar were computed.

Data were arranged in the form of a life table (Andrewartha and Birch 1954) for each *A. gossypii* cohort reared on each taro cultivar. Values for $l_x$ (proportion of cohort surviving) and $m_x$ (mean number of female offspring per female) were determined for each cultivar. Data for the probability of survival ($l_x$) and average number of progeny per female ($m_x$) were plotted against age for the top five resistant and top five susceptible cultivars. Data for the five most aphid-resistant and five most aphid-susceptible cultivars were pooled and plotted against age.

Life table statistics were derived using Poptools software developed by the University of Minnesota (http://www.cse.csiro.au/poptools/index.htm). The intrinsic rate of increase (r) was estimated by iteration of Euler–Lotka's equation $\Sigma\ e^{-rx} l_x m_x = 1$, where *r* is

**Table 2. Selected agronomic characteristics of taro cultivars**

| Cultivar | Plant ht | Leaf span | Leaf blade color | Leaf vein color | Petiole color | Leaf waxiness | Plant vigor |
|---|---|---|---|---|---|---|---|
| A. Pohntipw | Medium | Medium | Green | Green | Red | Low | Good |
| AG-1 | Medium | Narrow | Green | Green | Pink | Low | Poor |
| Agaga | Dwarf | Narrow | Dark green | Purple | Pink | Low | Poor |
| Apu-23 | Tall | Medium | Green | White | Pink | Med | Good |
| Bun Long | Medium | Medium | Dark green | Green | Purple | Low | Good |
| Dar 2 | Dwarf | Narrow | Green | Yellow-green | Pink | Low | Poor |
| Dar 3 | Medium | Medium | Green | Purple | Brown | Low | Good |
| Dar 4 | Medium | Narrow | Green | White | Dark green | Low | Poor |
| Dar 8 | Medium | Medium | Green | Green | Dark green | Low | Excellent |
| Dar 10 | Tall | Medium | Green | Purple | Purple | Low | Good |
| Dar 11 | Medium | Medium | Green | Green | Pink | Low | Excellent |
| Dar 12 | Medium | Medium | Dark green | Yellow-green | Purple | Low | Excellent |
| Fel | Medium | Medium | Green | Yellow-green | Pink | Medium | Excellent |
| Fiji | Medium | Medium | Green | Yellow-green | Dark green | Low | Good |
| Gilin | Medium | Medium | Green | Green | Dark green | Low | Good |
| Gurumed | Medium | Medium | Green | Green | Pink | Low | Good |
| Gutep | Medium | Medium | Green | Green | Pink | Low | Good |
| Hana | Tall | Medium | Green | Red | Red | Low | Good |
| Iliuaua | Medium | Medium | Green | White | Dark green | High | Excellent |
| Japon | Medium | Medium | Green | Purple | Red | Low | Good |
| John | Medium | Medium | Green | Green | Pink | Low | Good |
| Ketan 36 | Dwarf | Narrow | Green | Green | Pink | High | Good |
| Kosrae | Medium | Medium | Dark green | Red | Red | Medium | Good |
| Kugfel | Medium | Medium | Green | Purple | Purple | Medium | Excellent |
| Laatan Green | Medium | Medium | Green | Brown | Dark green | Low | Good |
| Laatan Red | Medium | Medium | Dark green | Pink | Red | Low | Excellent |
| Laev | Medium | Narrow | Green | Brown | Red | Low | Poor |
| Likay | Medium | Medium | Dark green | Green | Red | Low | Good |
| Mang | Tall | Medium | Green | Green | Purple | Medium | Excellent |
| Mang Green | Medium | Medium | Green | White | Pink | Low | Excellent |
| Mang Red | Medium | Medium | Green | Red | Purple | Medium | Excellent |
| Maria | Dwarf | Narrow | Yellow-green | Green | Pink | Low | Poor |
| Mat | Medium | Medium | Yellow-green | Purple | Red | Medium | Poor |
| Moy | Medium | Medium | Dark green | Green | Purple | Low | Excellent |
| Niue | Dwarf | Medium | Green | Green | Pink | Low | Good |
| Oglang | Tall | Medium | Dark green | Red | Purple | Low | Excellent |
| Okinawa | Tall | Narrow | Green | White | Dark green | Low | Excellent |
| Olyap | Medium | Medium | Green | Green | Pink | Medium | Good |
| P-10 | Medium | Medium | Green | Green | Dark green | Low | Good |
| P-20 | Tall | Medium | Dark green | Purple | Purple | Medium | Excellent |
| Purple | Dwarf | Medium | Purple | White | Purple | Low | Good |
| Putih 24 | Medium | Medium | Dark green | White | Dark green | Medium | Good |
| Pwetepwet | Medium | Medium | Green | White | Dark green | Medium | Good |
| Red Palauan | Medium | Medium | Dark Green | Purple | Brown | Medium | Excellent |
| Rumung 1 | Medium | Medium | Green | Red | Purple | Low | Excellent |
| Rumung John | Medium | Medium | Green | White | Pink | Low | Good |
| Rumung Lisa | Medium | Medium | Dark green | Red | Purple | Medium | Excellent |
| Rumung Mary | Medium | Medium | Dark green | Purple | Brown | Low | Good |
| Saipan | Medium | Medium | Dark green | Purple | Purple | Medium | Excellent |
| SPC | Medium | Medium | Green | Green | Dark green | Low | Good |
| Sushi | Medium | Medium | Dark green | Green | Pink | Low | Excellent |
| Tamdad | Medium | Medium | Green | White | Brown | Low | Good |
| Tamdad Yellow | Medium | Medium | Green | White | Pink | Low | Excellent |
| TC- 83001 | Dwarf | Narrow | Yellow-green | Green | Pink | Low | Good |
| Tinian | Tall | Medium | Dark green | Red | Purple | Medium | Good |
| Toantal | Medium | Medium | Dark green | Purple | Purple | Medium | Good |
| Visaya | Tall | Medium | Dark green | Purple | Purple | Medium | Excellent |
| White BL | Tall | Medium | Green | Red | Pink | Medium | Excellent |
| *X. sagittifolium* | Tall | Wide | Green | Green | Pink | Medium | Good |

the intrinsic rate of increase, $l_x$ is the proportion of individuals surviving to the start of age x, $m_x$ is the number of offspring produced per female at age x, and e is the base of the natural logarithm. Generation time T was then computed as $T = \Sigma x e^{-rx} l_x m_x$.

NCSS 2000 software (Hintze 2000) was used to compute means and standard errors of the mean and perform to other statistical procedures.

**Antixenosis Experiments.** A multiround single elimination choice experiment was conducted to test for preferences of *A. gossypii* toward the 59 cultivars (Fig. 1). Taro leaves intermediate in age were collected from four randomly chosen cultivars from the taro patch at the Yigo Experiment Station. Uniform 2-cm-diameter leaf disks were cut from each of four taro cultivars by using a cork borer and placed equi-

**Table 3. Abundance rankings of *A. gossypii* populations in the field on taro cultivars, and mean longevity and fecundity of apterous *A. gossypii* caged on taro cultivars**

| Cultivar | Sample size | Mean ± SE aphid density | Sample size | Mean (± SE) longevity (d) | Mean (± SE) fecundity (offspring/female) |
|---|---|---|---|---|---|
| *X. sagittifolium* | 5 | 0.20 ± 0.20 (1) | 14 | 11.4 ± 2.2 (3) | 6.4 ± 2.0 (1) |
| Iliuaua | 5 | 0.40 ± 0.24 (2) | 14 | 8.6 ± 2.5 (1) | 9.5 ± 4.1 (5) |
| TC-83001 | 5 | 0.40 ± 0.24 (2) | 14 | 19.1 ± 2.6 (18) | 21.2 ± 4.2 (15) |
| Dar 4 | 5 | 0.50 ± 0.29 (3) | 14 | 16.8 ± 2.5 (12) | 12.7 ± 2.8 (7) |
| Gutep | 5 | 0.60 ± 0.24 (4) | 11 | 21.3 ± 3.1 (33) | 24.5 ± 4.6 (27) |
| Apu-23 | 5 | 0.60 ± 0.24 (4) | 17 | 16.7 ± 2.7 (11) | 21.8 ± 5.4 (16) |
| Laatan Red | 5 | 0.60 ± 0.24 (4) | 10 | 19.6 ± 2.6 (23) | 25.9 ± 4.0 (30) |
| Bun Long | 5 | 0.60 ± 0.24 (4) | 18 | 20.1 ± 3.0 (28) | 24.4 ± 4.8 (26) |
| Fel | 5 | 0.60 ± 0.40 (4) | 13 | 15.4 ± 3.4 (7) | 24.3 ± 6.8 (25) |
| Okinawa | 5 | 0.60 ± 0.24 (4) | 13 | 22.5 ± 2.5 (39) | 23.7 ± 3.5 (24) |
| Ketan 36 | 5 | 0.60 ± 0.24 (4) | 12 | 14.0 ± 2.5 (5) | 10.0 ± 2.7 (6) |
| Agaga | 5 | 0.75 ± 0.25 (5) | 14 | 14.3 ± 2.3 (6) | 8.3 ± 2.1 (4) |
| SPC | 5 | 0.80 ± 0.20 (6) | 17 | 17.6 ± 2.2 (15) | 34.0 ± 5.5 (50) |
| Maria | 5 | 1.00 ± 0.41 (7) | 25 | 13.0 ± 1.8 (4) | 7.8 ± 1.8 (2) |
| AG-1 | 5 | 1.00 ± 0.41 (7) | 23 | 15.8 ± 1.4 (8) | 17.4 ± 2.9 (9) |
| Likay | 5 | 1.00 ± 0.32 (7) | 13 | 17.7 ± 2.4 (16) | 27.8 ± 5.4 (33) |
| Mang | 5 | 1.00 ± 0.32 (7) | 17 | 19.2 ± 2.4 (19) | 23.1 ± 3.9 (19) |
| Niue | 5 | 1.00 ± 0.45 (7) | 14 | 20.3 ± 2.5 (29) | 28.3 ± 4.8 (37) |
| Moyoyol | 5 | 1.20 ± 0.20 (8) | 15 | 19.6 ± 2.3 (25) | 20.8 ± 2.6 (12) |
| Olyap | 5 | 1.20 ± 0.20 (8) | 15 | 21.2 ± 2.4 (32) | 26.1 ± 3.6 (31) |
| Dar 12 | 5 | 1.20 ± 0.20 (8) | 13 | 20.7 ± 2.4 (30) | 23.5 ± 4.6 (21) |
| Mang Red | 5 | 1.20 ± 0.37 (8) | 10 | 25.5 ± 3.5 (50) | 31.2 ± 5.0 (44) |
| Tamdad Yellow | 5 | 1.20 ± 0.37 (8) | 13 | 22.6 ± 2.5 (40) | 41.5 ± 5.0 (56) |
| Putih 24 | 5 | 1.20 ± 0.20 (8) | 15 | 22.9 ± 2.3 (42) | 27.9 ± 4.1 (34) |
| Rumung Mary | 5 | 1.25 ± 0.25 (9) | 10 | 11.2 ± 2.6 (2) | 7.9 ± 3.2 (3) |
| Dar 10 | 5 | 1.25 ± 0.25 (9) | 17 | 19.4 ± 2.4 (21) | 21.8 ± 3.6 (16) |
| Hana | 5 | 1.25 ± 0.25 (9) | 13 | 22.9 ± 2.3 (42) | 28.0 ± 4.6 (35) |
| Purple | 5 | 1.25 ± 0.25 (9) | 14 | 23.1 ± 2.1 (43) | 23.3 ± 4.0 (20) |
| Tinian | 5 | 1.40 ± 0.40 (10) | 16 | 17.1 ± 2.5 (13) | 22.5 ± 4.5 (17) |
| Dar 8 | 5 | 1.40 ± 0.24 (10) | 33 | 19.9 ± 1.7 (26) | 24.6 ± 3.2 (28) |
| Fiji | 5 | 1.40 ± 0.24 (10) | 14 | 22.3 ± 2.6 (37) | 30.5 ± 4.6 (39) |
| Gilin | 5 | 1.40 ± 0.40 (10) | 17 | 24.1 ± 2.5 (47) | 44.7 ± 5.3 (57) |
| A. Ponhntipw | 5 | 1.40 ± 0.40 (10) | 20 | 20.0 ± 2.3 (27) | 28.2 ± 4.2 (36) |
| Rumung Lisa | 5 | 1.40 ± 0.24 (10) | 13 | 22.4 ± 1.7 (38) | 46.4 ± 4.1 (58) |
| Dar 2 | 5 | 1.50 ± 0.50 (11) | 22 | 17.8 ± 1.9 (17) | 15.1 ± 2.4 (8) |
| Mat | 5 | 1.50 ± 0.29 (11) | 14 | 21.7 ± 3.0 (35) | 20.4 ± 4.2 (11) |
| Gurumed | 5 | 1.60 ± 0.24 (12) | 15 | 20.0 ± 2.3 (27) | 30.8 ± 5.0 (42) |
| Dar 3 | 5 | 1.60 ± 0.24 (12) | 13 | 23.1 ± 2.3 (43) | 30.6 ± 4.7 (40) |
| P-10 | 5 | 1.60 ± 0.40 (12) | 16 | 21.6 ± 1.8 (34) | 41.3 ± 4.0 (55) |
| Laatan Green | 5 | 1.60 ± 0.51 (12) | 13 | 24.5 ± 2.6 (49) | 33.6 ± 5.6 (48) |
| Rumung 1 | 5 | 1.75 ± 0.25 (13) | 15 | 19.6 ± 2.0 (26) | 17.5 ± 3.7 (10) |
| Laev | 5 | 1.75 ± 0.25 (13) | 14 | 23.2 ± 2.1 (44) | 30.7 ± 4.7 (41) |
| Oglang | 5 | 1.80 ± 0.49 (14) | 24 | 16.1 ± 1.5 (9) | 22.8 ± 3.5 (18) |
| Sushi | 5 | 1.80 ± 0.37 (14) | 14 | 17.5 ± 2.7 (14) | 21.0 ± 5.8 (13) |
| Mang Green | 5 | 1.80 ± 0.20 (14) | 15 | 22.4 ± 2.2 (38) | 24.8 ± 4.1 (29) |
| Dar 11 | 5 | 1.80 ± 0.20 (14) | 13 | 23.3 ± 2.7 (45) | 31.1 ± 4.3 (43) |
| Tamdad | 5 | 1.80 ± 0.37 (14) | 13 | 24.4 ± 2.2 (48) | 35.7 ± 4.5 (53) |
| Rumung John | 5 | 1.80 ± 0.20 (14) | 15 | 22.2 ± 2.2 (36) | 33.7 ± 5.3 (49) |
| Red Palauan | 5 | 2.00 ± 0.41 (15) | 14 | 16.3 ± 2.6 (10) | 21.1 ± 5.7 (14) |
| Kugfel | 5 | 2.00 ± 0.32 (15) | 16 | 19.5 ± 1.8 (24) | 33.2 ± 3.9 (47) |
| Visaya | 5 | 2.00 ± 0.32 (15) | 16 | 20.8 ± 2.1 (31) | 32.5 ± 4.7 (45) |
| P-20 | 5 | 2.00 ± 0.32 (15) | 14 | 19.5 ± 2.2 (22) | 35.1 ± 5.3 (52) |
| White BL | 5 | 2.00 ± 0.32 (15) | 13 | 23.1 ± 2.3 (43) | 27.5 ± 4.8 (32) |
| Kosrae | 5 | 2.00 ± 0.32 (15) | 18 | 19.3 ± 2.0 (20) | 34.3 ± 5.0 (51) |
| Pwetepwet | 5 | 2.00 ± 0.45 (15) | 17 | 23.4 ± 1.8 (46) | 33.0 ± 3.6 (46) |
| Saipan | 5 | 2.00 ± 0.32 (15) | 15 | 22.8 ± 2.5 (41) | 23.6 ± 3.6 (22) |
| Japon | 5 | 2.25 ± 0.25 (16) | 14 | 21.7 ± 2.7 (35) | 23.6 ± 4.0 (23) |
| Toantal | 5 | 2.40 ± 0.24 (17) | 15 | 22.9 ± 2.3 (42) | 28.5 ± 4.5 (38) |
| John | 5 | 2.60 ± 0.24 (18) | 15 | 22.5 ± 2.1 (39) | 35.8 ± 5.1 (54) |
| | | H = 128.129[a] | | CV = 18.2 | CV = 34.7 |
| | | df = 58 | | $F_{(58,844)} = 2.29$**[b] | $F_{(58,844)} = 4.34$**[b] |
| | | $P \leq 0.001$ | | $LSD_{(0.05,\ 902)} = 6.47$ | $LSD_{(0.05,\ 902)} = 11.92$ |

Numbers in parentheses indicate the rank of a cultivar for that category.
[a] Kruskal–Wallis one-way analysis of variance on ranks for abundance data not normally distributed (Zar 1999).
[b] One-way analysis of variance, $^{**}P \leq 0.001$.

distant from one another on water-moistened Whatman filter paper no. 2 in a 100 by 15-mm petri dish with the upper surface of the leaf facing upward. Sixteen mature aphids were transferred with a fine sable brush to the moistened filter paper and placed in the middle of the filter paper equidistant from the four leaf discs.

Dishes were covered and randomly arranged on a laboratory bench for 24 h at 22°C and constant room lighting, at which time the location of the aphids was recorded. Each first- and second-round test involved four cultivar combinations and was replicated five times. Subsequent test rounds involved two cultivar combinations with two leaf disks per petri dish and also were replicated five times.

The cultivar with the highest total number of aphids after the 24-h time interval was advanced to subsequent rounds of testing against other aphid-preferred cultivars. Series of these tests lead to the identification of the most highly preferred, or least aphid-resistant, cultivar. Conversely, the cultivar on which the fewest aphids aggregated after the 24-h period was advanced and subsequently tested against other cultivars that had "won" their round. A series of these tests lead to the identification of the least-preferred, or most aphid-resistant, cultivar (Fig. 1). The entire experiment to identify "winners" and "losers" was repeated six times. The number of times a cultivar advanced to higher rounds (round 2 and higher) in either the least preferred or most preferred bracket was recorded. Overall resistance and susceptibility rankings for taro cultivars were based on the number of appearances in the more advanced rounds of the choice tests.

## Results

**Agronomic Characteristics.** There were observable differences in plant height, leaf span, leaf color, leaf vein color, petiole waxiness, and plant vigor characteristics among taro cultivars (Table 2). Seven cultivars grew poorly in Yigo, including 'AG-1', 'Agaga', 'Dar 12', 'Dar 4', 'Laev', 'Maria', and 'Mat'. Two, 'Iliuaua' and 'Ketan 36', possessed very waxy leaves, whereas 38 cultivars had leaves with low waxiness and 19 had medium waxiness.

**Naturally Occurring Abundance.** Field ratings of the naturally occurring abundance of *A. gossypii* differed among taro cultivars grown at the Yigo Agricultural Experiment Station (Table 3). Depending on the time of planting of the cultivar, either four or five observations were made at ≈1-mo intervals. No aphids were observed on *X. sagittifolium* in four out of five scoring episodes, and on the last scoring date only 0.2 aphid per leaf were observed. Iliuaua, 'TC-83001', Dar 4, and *X. sagittifolium* were the only taros with low naturally occurring abundance. Cultivars exhibiting a mean rating >2.0 for naturally occurring aphid abundance included 'Japon', 'Toantal', and 'John'.

**Antibiosis.** Mean adjusted *A. gossypii* longevity ranged from 8.6 d when caged on Iliuaua to 25.5 d when caged on 'Mang Red' (Table 3). Caged aphids were the most short-lived on Iliuaua, 'Rumung Mary', *X. sagittifolium,* 'Maria', and 'Ketan 36'. Caged aphids lived longest on Mang Red, 'Laatan Green', 'Tamdad', 'Gilin', and 'Pwetepwet'. Pairwise comparisons revealed significant differences between longevity in the most susceptible and most resistant cultivars.

Mean fecundity of *A. gossypii* ranged from 6.4 offspring when caged on *X. sagittifolium* to 46.4 offspring when caged on 'Rumung Lisa' (Table 3). Caged *A. gossypii* were the least fecund on *X. sagittifolium,* Maria, Rumung Mary, 'Agaga', and Iliuaua. Aphids on Ketan 36, ranked sixth, did not significantly differ in mean fecundity from the top five cultivars. Caged aphids demonstrated the greatest mean fecundity on Rumung Lisa, Gilin, 'Tamdad Yellow', 'P-10', and John. All aphid populations on these cultivars differed significantly from those on the six cultivars exhibiting the lowest mean fecundity.

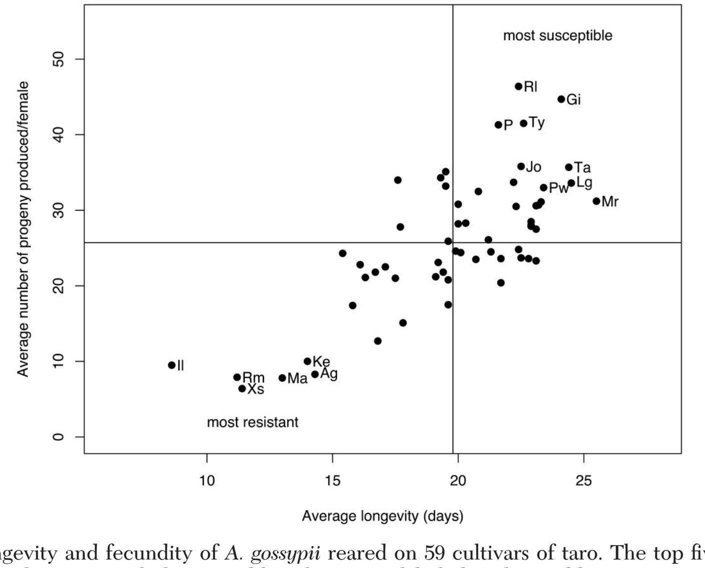


**Fig. 2.** Average longevity and fecundity of *A. gossypii* reared on 59 cultivars of taro. The top five aphid-resistant taro cultivars, *Xanthosoma*, and top nine aphid-susceptible cultivars are labeled. Cultivar abbreviations are as follows: Il, Iliuaua; Rm, Rumung Mary; Xs, *Xanthosoma*; Ma, Maria; Ke, Ketan 36; Ag, Agaga; Mr, Mang Red; Lg, Laatan Green; Pw, Pwetepwet; Ta, Tamdad; Jo, John; Ty, Tamdad Yellow; P, P-10; Gi Gilin; Rl, Rumung Lisa.

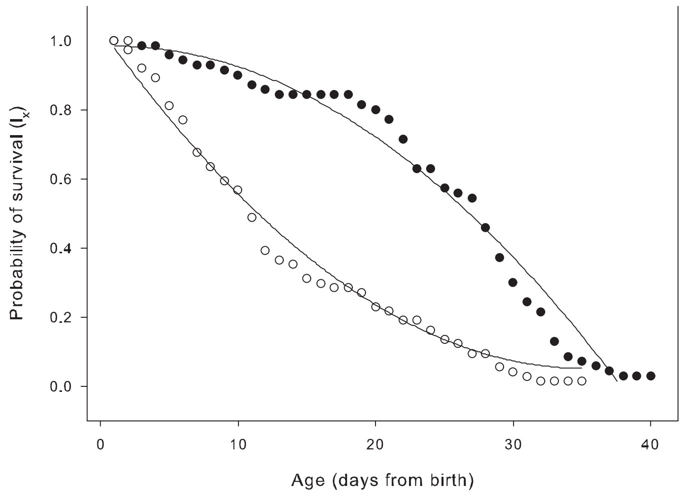


**Fig. 3.** Age-specific survivorship ($l_x$) patterns of *A. gossypii* confined to clip cages on the top five aphid-resistant (open circles) and aphid-susceptible (closed circles) taro cultivars. Aphid-resistant cultivars included Iliuaua, Ketan 36, Agaga, Rumung Mary, and Maria, whereas aphid-susceptible cultivars included Pwetepwet, Gilin, Tamdad, Laatan Green, and Mang Red.

The average longevity of caged aphids was positively correlated to the average number of offspring produced per female (Fig. 2). Aphids caged on the aphid-resistant Iliuaua, Rumung Mary, *X. sagittifolium,* Maria, Ketan 36, and Agaga demonstrated the lowest offspring production and shortest survival. These cultivars as well as others in the lower left quadrant exhibited both a reduction in longevity and fecundity. Conversely, aphids in the upper right quadrant demonstrated high offspring production and long survival. The most susceptible among these cultivars were Mang Red, Laatan Green, Pwetepwet, Tamdad, John, Tamdad Yellow, P-10, Gilin, and Rumung Lisa. Values for other cultivars falling in the upper left quadrant (below average longevity, above average fecundity) and in the lower right quadrant (above average longevity, below average fecundity) and that clustered near the means for both axes may be considered moderately aphid-resistant or susceptible.

Mean age-specific survivorship ($l_x$) patterns of aphid cohorts reared on the five most resistant taro cultivars and *X. sagittifolium* and the five most susceptible taro cultivars were plotted (Fig. 3). Aphid survivorship on resistant cultivars corresponded to a type III survivorship curve where high mortality occurred early in life and then tapered off. The pattern of survivorship of aphids caged on susceptible cultivars, however, followed a type I survivorship curve by exhibiting low mortality early in life and greater mortality among older aphids (Pearl 1927, Deevey 1947).

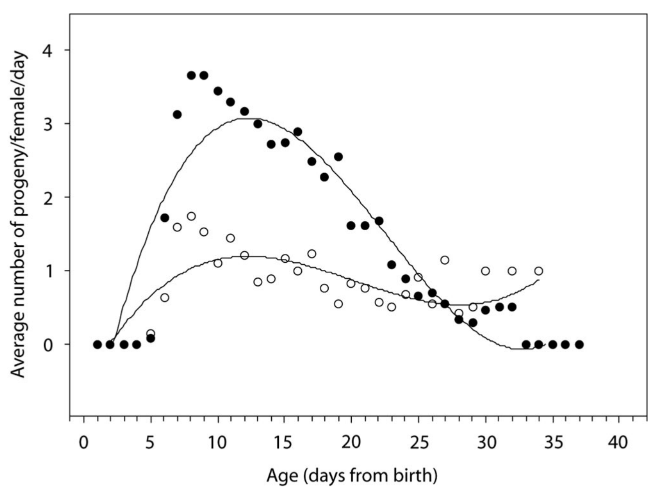


**Fig. 4.** Age-specific fecundity ($m_x$) patterns of *A. gossypii* confined to clip cages on the top five pooled aphid-resistant (open circles) and aphid-susceptible (closed circles) taro cultivars. Aphid-resistant cultivars included Iliuaua, Ketan 36, Agaga, Rumung Mary, and Maria, whereas susceptible cultivars included John, P-10, Tamdad Yellow, Gilin, and Rumung Lisa.

Mean age-specific fecundity ($m_x$) of aphid cohorts reared on the five most resistant taro cultivars and *X. sagittifolium,* and on the five most susceptible taro cultivars were plotted (Fig. 4). Most aphids began reproducing at 5 or 6 d of age on both resistant and susceptible cultivars. Fecundity peaked 4–6 d later.

Aphid fecundity peaked at nine days on resistant cultivars with peak fecundity averaging ≈2.5 progeny per female. Aphid fecundity peaked near 11 d on susceptible cultivars, with peak fecundity averaging about four progeny per female.

Overall, fecundity patterns of aphids on resistant cultivars were more erratic than on susceptible cultivars as the number of progeny produced frequently dropped to zero for many of the cultivars once aphids were 15 d old or older. Aphid fecundity on susceptible cultivars did not drop to zero on any of the five cultivars until several days later.

**Life Table Statistics.** Positive intrinsic rates of increase, or the change in population size per individual per unit of time denoted by r, indicate increasing populations on all cultivars and for *X. sagittifolium* (Table 4). Values of *r* ranged from 0.137 for *X. sagittifolium* to 0.439 for Rumung Lisa. Lower intrinsic rates of increase were consistent with host cultivars in which aphids exhibited the lowest fecundity and longevity.

Generation times were similar among aphids reared on the various cultivars, with the range among cultivars being 2.4 d. There was no correlation between generation times and the other antibiosis parameters evaluated.

**Antixenosis.** Summing the number of appearances in advanced rounds of the multiple-round tests from six separate trials allowed the identification and ranking of the least preferred (Table 5) and most preferred cultivars (Table 6). Iliuaua was the least preferred cultivar in four of six trials. In two of six trials, Purple was the least preferred cultivar and ranked second overall. TC-83001, *X. sagittifolium,* and Putih 24 rounded out the five least-preferred cultivars. Moyoyol and P-20 were each preferred by aphids in two of six trials, and P-10 and Laatan Green were each preferred in one of six trials.

## Discussion

**Environmental Conditions.** A number of environmental factors affected data collection during the study. In July and December 2002, typhoons Chata'an and Pongsona struck Guam with winds in excess of 200 km/h and rainfall measuring >50 cm in a 24-h period. Aphid populations were low for several weeks after each typhoon until plant communities had fully reestablished. At other times, nontyphoon wind gusts in excess of 40 km/h tore taro leaves where clip cages were attached and blew both aphid and cage from the plant. Heavy rains at the beginning of the field study in January 2002 and in May and June 2002 resulted in the loss of some clip cages, and aphids sometimes drowned within the cages as rainwater became trapped inside the cage. Ants sometimes cut through the screen of the clip cage and removed the adult aphid. The effect of biotic and abiotic factors was resolved by excluding data from these cages from the analysis.

**Table 4. Intrinsic rate of increase (*r*) and generation time (T) of *A. gossypii* caged on different taro cultivars**

| Cultivar | *r* | SE | Cultivar | T | SE |
|---|---|---|---|---|---|
| *X. sagittifolium* | 0.137 | 0.072 | Mang Green | 8.750 | 1.953 |
| Maria | 0.202 | 0.023 | SPC | 8.506 | 0.473 |
| Rumung Mary | 0.243 | 0.011 | Laatan Green | 8.441 | 0.001 |
| Iliuaua | 0.248 | 0.063 | Gilin | 8.434 | 0.711 |
| Ketan 36 | 0.281 | 0.037 | Maria | 8.420 | 0.274 |
| Agaga | 0.281 | 0.071 | Okinawa | 8.390 | 0.954 |
| Niue | 0.282 | 0.025 | Niue | 8.386 | 0.331 |
| Okinawa | 0.289 | 0.057 | Bun Long | 8.269 | 0.482 |
| Dar 2 | 0.292 | 0.037 | *X. sagittifolium* | 8.204 | 0.799 |
| Mat | 0.296 | 0.034 | Gutep | 8.169 | 0.543 |
| Saipan | 0.296 | 0.040 | Fel | 8.145 | 0.199 |
| Dar 4 | 0.299 | 0.035 | Dar 11 | 8.041 | 0.388 |
| Bun Long | 0.301 | 0.017 | Hana | 8.024 | 0.631 |
| TC-83001 | 0.304 | 0.013 | Iliuaua | 8.008 | 0.150 |
| Gutep | 0.307 | 0.044 | Mat | 7.887 | 0.537 |
| Rumung 1 | 0.307 | 0.036 | Mang Red | 7.878 | 0.579 |
| Laatan Green | 0.309 | 0.022 | Gurumed | 7.863 | 0.621 |
| Japon | 0.314 | 0.014 | Apu-23 | 7.774 | 0.301 |
| Mang Green | 0.314 | 0.073 | Japon | 7.698 | 0.276 |
| Fel | 0.318 | 0.014 | Mang | 7.689 | 0.202 |
| Mang Red | 0.324 | 0.019 | Sushi | 7.584 | 0.264 |
| Dar 11 | 0.327 | 0.007 | Dar 3 | 7.574 | 0.340 |
| Red Palauan | 0.327 | 0.012 | Olyap | 7.559 | 0.417 |
| AG 1 | 0.328 | 0.024 | Rumung 1 | 7.545 | 0.301 |
| Apu-23 | 0.328 | 0.028 | Kugfel | 7.501 | 0.315 |
| Hana | 0.328 | 0.014 | Purple | 7.415 | 0.203 |
| Sushi | 0.328 | 0.031 | Laev | 7.405 | 1.170 |
| Mang | 0.330 | 0.013 | Rumung John | 7.395 | 0.431 |
| Purple | 0.333 | 0.013 | Dar 8 | 7.383 | 0.370 |
| Moyoyol | 0.335 | 0.008 | TC-83001 | 7.376 | 0.095 |
| Olyap | 0.343 | 0.012 | Dar 2 | 7.350 | 0.405 |
| Dar 12 | 0.344 | 0.011 | Tamdad | 7.344 | 0.417 |
| Dar 8 | 0.344 | 0.026 | Kosrae | 7.307 | 0.557 |
| Tinian | 0.346 | 0.016 | Red Palauan | 7.286 | 0.240 |
| Putih-24 | 0.347 | 0.006 | White BL | 7.264 | 0.384 |
| Dar 3 | 0.353 | 0.027 | Dar 12 | 7.211 | 0.075 |
| White BL | 0.353 | 0.006 | Pwetepwet | 7.209 | 0.517 |
| Laatan Red | 0.358 | 0.014 | Putih-24 | 7.206 | 0.170 |
| Gurumed | 0.361 | 0.038 | Laatan Red | 7.144 | 0.617 |
| Dar 10 | 0.362 | 0.013 | A. Ponhntipw | 7.143 | 0.213 |
| Rumung John | 0.367 | 0.007 | P-20 | 7.120 | 0.361 |
| Pwetepwet | 0.368 | 0.040 | Ketan 36 | 7.090 | 0.266 |
| Toantal | 0.372 | 0.046 | Moyoyol | 7.072 | 0.148 |
| Fiji | 0.373 | 0.056 | AG 1 | 7.030 | 0.233 |
| Laev | 0.376 | 0.061 | Visaya | 7.015 | 0.362 |
| A. Ponhntipw | 0.382 | 0.040 | John | 6.988 | 0.195 |
| Likay | 0.382 | 0.052 | P-10 | 6.975 | 0.059 |
| Kugfel | 0.387 | 0.018 | Rumung Mary | 6.970 | 0.504 |
| Visaya | 0.389 | 0.023 | Toantal | 6.957 | 0.190 |
| Oglang | 0.392 | 0.031 | Fiji | 6.943 | 0.603 |
| P-20 | 0.397 | 0.020 | Saipan | 6.841 | 0.238 |
| Tamdad Yellow | 0.399 | 0.016 | Dar 10 | 6.831 | 0.702 |
| Kosrae | 0.402 | 0.048 | Tinian | 6.826 | 0.021 |
| SPC | 0.408 | 0.011 | Tamdad Yellow | 6.765 | 0.523 |
| Gilin | 0.409 | 0.046 | Oglang | 6.659 | 0.262 |
| Tamdad | 0.409 | 0.028 | Dar 4 | 6.627 | 0.130 |
| John | 0.414 | 0.016 | Rumung Lisa | 6.609 | 0.207 |
| P-10 | 0.427 | 0.011 | Agaga | 6.490 | 0.940 |
| Rumung Lisa | 0.439 | 0.004 | Likay | 6.352 | 0.516 |

Values for *r* were computed from life history data in which the suspected cause of mortality of caged *A. gossypii* was natural and not the result of extraneous factors. Taro cultivars are ordered from lowest to highest based on *r* values.

**Agronomic Characteristics.** There were differences in leaf blade color, leaf vein color, and petiole color

**Table 5. Results of antixenosis experiments identifying the most aphid resistant taro cultivars (nonpreferred)**

| Cultivar PROB | Round no. 2 0.25 | 3 0.0625 | 4 0.03125 | Final 0.015625 | Total | Cultivar PROB | Round no. 2 0.25 | 3 0.0625 | 4 0.03125 | Final 0.015625 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Iliuaua | 6 | 5 | 4 | 4[a] | 19 | Rumung 1 | 1 | | | | 1 |
| Purple | 4 | 3 | 2 | 2[b] | 11 | Olyap | 1 | | | | 1 |
| TC-83001 | 5 | 3 | 2 | | 10 | Niue | 1 | | | | 1 |
| *X. sagittifolium* | 3 | 3 | 2 | | 8 | Mat | 1 | | | | 1 |
| Putih 24 | 4 | 2 | 1 | | 7 | Gurumed | 1 | | | | 1 |
| Gutep | 4 | 1 | 1 | | 6 | Kugfel | 1 | | | | 1 |
| Laatan Red | 4 | 2 | | | 6 | Visaya | 1 | | | | 1 |
| Maria | 3 | 1 | | | 4 | Mang Red | 1 | | | | 1 |
| Sushi | 3 | 1 | | | 4 | Dar 8 | 1 | | | | 1 |
| Hana | 3 | 1 | | | 4 | Japon | 1 | | | | 1 |
| Rumung Mary | 4 | | | | 4 | Fiji | 1 | | | | 1 |
| Kosrae | 2 | 1 | | | 3 | Gilin | 1 | | | | 1 |
| Agaga | 3 | | | | 3 | A. Ponhntipw | 1 | | | | 1 |
| Dar 4 | 3 | | | | 3 | Dar 3 | 1 | | | | 1 |
| SPC | 3 | | | | 3 | Laatan Green | 1 | | | | 1 |
| Pwetepwet | 3 | | | | 3 | Rumung Lisa | 1 | | | | 1 |
| Red Palauan | 1 | 1 | | | 2 | Tamdad Yellow | 1 | | | | 1 |
| AG-1 | 2 | | | | 2 | Tamdad | 1 | | | | 1 |
| Mang | 2 | | | | 2 | Rumung John | 1 | | | | 1 |
| Dar 12 | 2 | | | | 2 | Ketan 36 | 0 | | | | 0 |
| White BL | 2 | | | | 2 | Bun Long | 0 | | | | 0 |
| Laev | 2 | | | | 2 | Okinawa | 0 | | | | 0 |
| John | 2 | | | | 2 | Dar 10 | 0 | | | | 0 |
| Apu-23 | 1 | | | | 1 | P-20 | 0 | | | | 0 |
| Likay | 1 | | | | 1 | Saipan | 0 | | | | 0 |
| Dar 2 | 1 | | | | 1 | P-10 | 0 | | | | 0 |
| Moyoyol | 1 | | | | 1 | Mang Green | 0 | | | | 0 |
| Oglang | 1 | | | | 1 | Dar 11 | 0 | | | | 0 |
| Fel | 1 | | | | 1 | Toantal | 0 | | | | 0 |
| Tinian | 1 | | | | 1 | | | | | | |

Column numbers reflect the number of times a taro cultivar occurred in the advanced rounds of the winner's bracket. PROB is the probability of any cultivar achieving a given round assuming the null hypothesis that there are no effects due to preference among cultivars.

[a] Probability of a cultivar "winning" four times in final round is $8.6 \times 10^{-7}$ computed as ${}_6C_4(p^4q^2)$, where p = 0.015625 and q = (1 − p) = 0.985.

[b] Probability of a cultivar winning twice in final round is $3.4 \times 10^{-3}$ computed as ${}_6C_2(p^2q^4)$, where $P$ = 0.015625 and q = (1–p) = 0.985.

observed between taro cultivars. Plant vigor, and to some degree plant height and leaf color, may result from local growing conditions, climate, and nutrient requirements unique to a cultivar. *A. gossypii* are attracted to red, orange, and yellow light rays with wavelengths of 610–570 nm and repelled by blue and violet light with wavelengths of 485–520 nm (Auclair 1969). Although aphids caged on the Purple, with its deep purple leaf blades and petioles, demonstrated high longevity and moderate fecundity in the field, aphids exhibited a high degree of nonpreference for Purple in the antixenosis experiments. Because excised leaves used in choice experiments included the leaf blade and no part of the leaf vein, the contrasting color combinations between leaf blade and leaf vein and petioles observed in the field were not represented.

Leaf waxiness may interfere with aphid stylet penetration into the leaf, thereby curbing feeding and affecting aphid performance. Plant surface characteristics of rice, including specific hydrocarbon fractions in leaf wax, have been shown to be partially responsible for resistance against phloem-feeding brown planthoppers (Woodhead and Padgham 1988). Iliuaua and Ketan 36 had very waxy leaves, and aphids on both cultivars exhibited low mean longevity and low mean fecundity.

**Naturally Occurring Abundance.** Assuming that colonizing alatae have an equal chance of locating taro cultivars, observed differences in aphid abundance in the field reflect differences in aphid preference for the taro cultivars. Once aphids have successfully colonized a host plant, differences in aphid abundance can be explained by greater rates of population increase on susceptible cultivars than on resistant cultivars. Mitigating factors that effect aphid abundance over time include abiotic factors such as rain and wind as well as biotic influences such as the presence of natural enemies.

In this study as well as in Miller and Wall (1999), mean abundance of *A. gossypii* was low on *X. sagittifolium* and high on the *Colocasia* Japon and Toantal. Iliuaua and TC-83001 exhibited low natural abundance of aphids in this study, but they were not examined by Miller and Wall (1999).

**Antibiosis.** Life history traits for *A. gossypii* reared on the 58 cultivars of taro and *X. sagittifolium* differed significantly (Table 3). Observed differences in aphid survival and fecundity are the basis for assessing antibiosis to *A. gossypii* in this study and may be explained by differences in the host plant's suitability for the aphid. The taro cultivars demonstrating the greatest reduction in aphid longevity were Iliuaua, Rumung Mary, Maria, Ketan 36, and Agaga, which also exhibited the greatest reduction in aphid fecundity. The low reproductive output of aphids caged on resistant taro cultivars is largely attributable to poor survivorship of

**Table 6. Results of antixenosis experiments for the most aphid-susceptible taro cultivars (preferred)**

| Cultivar PROB | Round no. | | | | | Cultivar PROB | Round no. | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2<br>0.25 | 3<br>0.0625 | 4<br>0.03125 | Final<br>0.015625 | Total | | 2<br>0.25 | 3<br>0.0625 | 4<br>0.03125 | Final<br>0.015625 | Total |
| Moyoyol | 4 | 2 | 2 | 2[a] | 10 | White BL | 2 | | | | 2 |
| P-20 | 3 | 2 | 2 | 2[a] | 9 | Saipan | 2 | | | | 2 |
| P-10 | 4 | 2 | 1 | 1[b] | 8 | Tamdad Yellow | 2 | | | | 2 |
| Laatan Green | 3 | 1 | 1 | 1[b] | 6 | Toantal | 2 | | | | 2 |
| Rumung Lisa | 4 | 2 | | | 6 | Rumung John | 2 | | | | 2 |
| Agaga | 3 | 1 | 1 | | 5 | Laev | 2 | | | | 2 |
| Kugfel | 3 | 1 | 1 | | 5 | Maria | 1 | | | | 1 |
| Mang Green | 4 | 1 | | | 5 | Gutep | 1 | | | | 1 |
| Dar 10 | 2 | 1 | 1 | | 4 | Dar 2 | 1 | | | | 1 |
| Dar 12 | 2 | 1 | 1 | | 4 | Tinian | 1 | | | | 1 |
| Mat | 2 | 1 | 1 | | 4 | Red Palauan | 1 | | | | 1 |
| John | 2 | 1 | 1 | | 4 | Niue | 1 | | | | 1 |
| Oglang | 2 | 1 | | | 3 | Visaya | 1 | | | | 1 |
| Rumung 1 | 2 | 1 | | | 3 | Gilin | 1 | | | | 1 |
| Dar 3 | 2 | 1 | | | 3 | Hana | 1 | | | | 1 |
| Dar 11 | 2 | 1 | | | 3 | *X. sagittifolium* | 0 | | | | 0 |
| Gurumed | 3 | | | | 3 | Rumung Mary | 0 | | | | 0 |
| Tamdad | 3 | | | | 3 | Iliuaua | 0 | | | | 0 |
| Ketan 36 | 1 | 1 | | | 2 | TC-83001 | 0 | | | | 0 |
| Apu-23 | 1 | 1 | | | 2 | Dar 4 | 0 | | | | 0 |
| Bun Long | 1 | 1 | | | 2 | Laatan Red | 0 | | | | 0 |
| Olyap | 1 | 1 | | | 2 | Likay | 0 | | | | 0 |
| AG-1 | 2 | | | | 2 | SPC | 0 | | | | 0 |
| Mang | 2 | | | | 2 | Sushi | 0 | | | | 0 |
| Okinawa | 2 | | | | 2 | Purple | 0 | | | | 0 |
| Fel | 2 | | | | 2 | A. Ponhntipw | 0 | | | | 0 |
| Mang Red | 2 | | | | 2 | Kosrae | 0 | | | | 0 |
| Dar 8 | 2 | | | | 2 | Pwetepwet | 0 | | | | 0 |
| Japon | 2 | | | | 2 | Putih 24 | 0 | | | | 0 |
| Fiji | 2 | | | | 2 | | | | | | |

Column numbers reflect the number of times a taro cultivar occurred in the advanced rounds of the loser's bracket. PROB is the probability of any cultivar achieving a given round assuming the null hypothesis that there are no effects due to preference among cultivars.

[a] Probability of a cultivar "losing" twice in final round is $3.4 \times 10^{-3}$ computed as ${}_6C_2(p^2q^4)$, where p = 0.015625 and q = (1 − p) = 0.985.

[b] Probability of a cultivar losing once in final round is 0.087 computed as ${}_6C_1(p^2q^4)$, where $P$ = 0.015625 and q = (1–p) = 0.985.

young aphids. The pooled survivorship curve of aphids reared on resistant taro cultivars demonstrates extensive mortality in early instars. Furthermore, aphids that survived through the reproductive period and were reared on resistant cultivars demonstrated low age-specific fecundity.

The most aphid susceptible taro cultivars in terms of aphid longevity, Mang Red, Laatan Green, Tamdad, and Pwetepwet, differed from those in which caged aphids exhibited the highest fecundity, Rumung Lisa, Tamdad Yellow, P-10, and John. Only Gilin showed high susceptibility to aphids both in longevity and fecundity (Table 3). Caged aphids demonstrated the same average prereproductive period of ≈5.5 d when reared on both groups of susceptible cultivars. Aphids on Mang Red, Laatan Green, Tamdad, Gilin, and Pwetepwet exhibited an average of >30 reproductive days, whereas the group with the highest computed fecundity, Rumung Lisa, Gilin, Tamdad Yellow, P-10, and John, were reproductively active for an average of ≈25 d.

**Life Table Statistics.** Overall performance of *A. gossypii* on different taro cultivars and *X. sagittifolium* was assessed by estimating *r*, the intrinsic rate of increase, for aphids on each cultivar. Values of *r* in this study, which ranged from 0.137 to 0.439 are near those reported by Perng (2002) for *A. gossypii* on *Solanum nigrum* L. (Solanaceae, *r* = 0.527), *Ageratum houstonianum* Mill (Asteraceae, *r* = 0.356), *Bidens pilosa* L. (Asteraceae, *r* = 0.272), and *Spermacoce latifolia* Aublet (Rubiaceae, *r* = 0.194).

Cole (1954) studied the relative effect on the intrinsic rate of increase when different life history parameters were altered and found *r* to be most sensitive to changes in maturation time or age at first reproduction and somewhat sensitive to birth rate. Consistent with the conclusions of Cole (1954), the Perng (2002) study of *A. gossypii* reared on four species of weeds found that the primary factors determining the value of *r* were the length of the prereproductive period and the magnitude of $m_x$. In this study, however, the developmental rate remained consistent for all aphids reared on all cultivars at either 5 or 6 d at first reproduction. The life history parameter having the greatest impact on the intrinsic rate of increase therefore was fecundity. The five taro cultivars exhibiting the lowest fecundity also had the lowest values for *r*. Conversely, those cultivars exhibiting the highest fecundity had the highest values for *r*.

**Antixenosis.** When given a free choice of hosts, aphids are assumed to avoid host cultivars on which survival and reproduction are inhibited and select cultivars for which these life history parameters are optimized. In this study a multiround choice test modeled after a single elimination sports tournament with excised taro leaves from two paired taro cultivars in each "competitive" round was used to identify a winner, or the most resistant cultivar, and a loser, or the most susceptible cultivar.

*A.gossypii* demonstrated low fecundity and survivorship when caged on *X. sagittifolium* and taro Iliuaua, which also were less preferred. Maria, Rumung Mary, Agaga, and Ketan 36 ranked among the top five for antibiosis but did not rank high for antixenosis. Purple, TC-83001, and Putih 24 exhibited intermediate levels of antibiosis but were ranked in the top five for antixenosis. TC-83001 is an example of a host in which antibiosis and antixenosis resistance mechanisms were not coupled because aphids exhibited intermediate fecundity and survivorship, but they showed low naturally occurring abundance and low preference. Results of the multiround choice test for preference also were not consistent with the antibiosis results. A cultivar demonstrating intermediate antibiosis resistance, Moyoyol, was one of two most preferred cultivars. The other most preferred cultivar, P-20, showed intermediate longevity and fecundity.

Iliuaua was consistently rated highly resistant in field and laboratory ratings for antixenosis, and for antibiosis, as was *X. sagittifolium.* TC-83001, Gutep, and Lataan Red also were ranked highly for nonpreference in field observations and in laboratory tests, but they were ranked lower and exhibited more inconsistency with regards to longevity or fecundity.

*C. esculenta,* typically vegetatively propagated, does not normally flower on Guam. Cooler temperatures in Maui, HI, promote flowering in taro and allows conventional crossing of aphid-resistant and aphid-susceptible lines. Segregation patterns in subsequent F1 and F2 generations can then be compared with patterns of expressed insect resistance, allowing for the identification of molecular markers. The identification of molecular markers, widely used in breeding programs, may increase the efficiency of screening and selection of resistant taro cultivars. Isozyme analysis of 1,417 cultivars and wild forms of taro by Lebot and Aradhya (1991) revealed that the greatest genetic diversity of taro occurs in Indonesia and the least diversity is found in Oceania. This genetic diversity can be exploited as necessary in future pest and disease research in taro to complement the sources of aphid resistance identified in this study.

## Acknowledgments

We thank Nenita Dumaliang, Lance VanderVelde, and Glen Meno for providing assistance in field preparation and data collection. Aubrey Moore and Gadi Reddy reviewed the manuscript, and John Brown, Carl Swanson, and Henry Taijerone provided additional constructive suggestions for data analysis. Funds for this project were provided by a USDA–TSTAR Special Projects grant.

## References Cited

**Adams, J. B., and H. F. van Emden. 1972.** The biological properties of aphids and their host plant relationships, pp. 47–104. *In* H. F. van Emden [ed.], Aphid technology. Academic, London, United Kingdom.

**Andrewartha, H. G., and L. C. Birch. 1954.** The distribution and abundance of animals. University of Chicago Press, Chicago, IL.

**Auclair, J. L. 1969.** Nutrition of plant-sucking insects on chemically defined diets. Entomol. Exp. Appl. 12: 623–641.

**Cole, L. C. 1954.** The population consequences of life history phenomena. Q. Rev. Biol. 29: 103–137.

**Deevey, E. S. 1947.** Life tables for natural populations of animals. Q. Rev. Biol. 22: 283–314.

**Ferentinos, L. 1993.** Proceedings of the Sustainable Taro Culture for Pacific Conference, 24–25 September 1992, East-West Center, Honolulu, HI. College of Tropical Agriculture and Human Resources. University of Hawaii, Manoa, HI.

**Hintze, J. L. 2000.** NCSS 2000, user's guide –1, statistical system for Windows. Number Cruncher Statistical Systems. Kaysvell, UT.

**Lebot, V., and K. M. Aradhya. 1991.** Isozyme variation in taro (*Colocasia esculenta* (L.) Schott) from Asia and Oceania. Euphytica 56: 55–66.

**Miller, R. H., and G. C. Wall. 1999.** Identification of sources of resistance against *Aphis gossypii* Glover (Homoptera: Aphididae) in taro, *Colocasia esculenta* (L). J. South Pac. Agric. 6: 26–33.

**Mitchell, W. C., and P. A. Maddison. 1983.** Pests of taro, pp. 180–235. *In* J. K. Wang [ed.], A review of *Colocasia esculenta* and its potentials. University of Hawaii Press, Honolulu, HI.

**Onwueme, I. 1999.** Taro cultivation in Asia and the Pacific. FAO Regional Office for Asia and the Pacific, Bangkok. Publ. No. 1999.16.

**Pearl, R. 1927.** The growth of populations. Q. Rev. Biol. 2: 532–548.

**Perng, J. J. 2002.** Life history traits of *Aphis gossypii* Glover (Hom., Aphididae) reared on four widely distributed weeds. J. Appl. Entomol. 126: 97–100.

**Rubatzky, V. E., and M. Yamaguchi. 1997.** Edible aroids, pp. 183–203. *In* V. E. Rubatzky and M. Yamaguchi [eds.], World vegetables, principles, production and nutritive values. Chapman & Hall, New York.

**Sokal, R. R., and F. J. Rohlf. 1995.** Biometry. W.H. Freeman and Company, New York.

**[SPC] South Pacific Commission. 1996.** Seminar on Pacific plant pathology in the 1990s, 5–7 September 1991, Suva, Fiji. Report. South Pacific Commission. Noumea, New Caledonia.

**Starý, P. 1970.** Biology of aphid parasites (Hymenoptera: Aphidiidae) with respect to integrated control. Series Entomologica, vol. 6. The Hague, The Netherlands.

**Sylvester, E. S. 1989.** Viruses transmitted by aphids, pp. 65–87. *In* A. K. Minks and P. Harrewijin [eds.], Aphids, their biology, natural enemies and control. vol. 2C. Elsevier, Amsterdam, The Netherlands.

**Woodhead, S., and D. E. Padgham. 1988.** The effect of plant surface characteristics on resistance of rice to the brown planthopper, *Nilaparvata lugens.* Entomol. Exp. Appl. 47: 15–22.

**Young, F. J. 1988.** Soil survey of territory of Guam. U.S. Dep. Agric. Soil Conserv. Serv. Agana, Guam.

**Zar, J. H. 1999.** Biostatistical analysis, 4th ed. Prentice-Hall, Upper Saddle River, NJ.

**Zettler, F. W., M. M. Abo El-Nil, and R. D. Hartman. 1978.** Dasheen mosaic virus. CMI/AAB Descriptions of Plant Viruses No. 191. Commonwealth Agricultural Bureaux. Kew, United Kingdom.

*Received 9 September 2004; accepted 7 January 2005.*